J. HYM. RES.
Vol. 9(1), 2000, pp. 53–61

The Biology of *Thrincohalictus prognathus* (Perez) (Hymenoptera: Halictidae: Halictini)

Laurence Packer

Department of Biology, York University, 4700 Keele St., Toronto, ON, M3J 1P3, Canada;
E-mail: bugsrus@yorku.ca

Abstract.—The Halictine bee *Thrincohalictus prognathus* (Perez) was studied in Israel in May and the beginning of June, 1998. Additional information was obtained from museum specimens. The species appears to be both common and widespread in northern Israel, particularly in the Galilee and Golan Heights where it occurs between altitudes of several hundred metres up to 1650m on Mount Hermon. Despite having an unusually elongate head, the species visits a wide range of flowers which generally do not possess a long corolla. Like most temperate halictines, only mated females overwinter and become active in the spring, as early as mid March. Males are found no earlier than mid May. The apparent age of females increases from March to May with newly eclosed, unworn individuals appearing in late May/early June. All worn early summer individuals were mated and had well developed ovaries. Thus, ovarian development and phenological data are inconsistent with the species being eusocial but are consistent with it being univoltine. The behaviour exhibited by paired females in artificial observation arenas indicates that *T. prognathus* possesses the repertoire of agonistic and cooperative behaviours usually found in halictines but that aggressive interactions predominate. Comparisons with other species indicate that the relative frequency of passing behaviour is very low and inconsistent with that expected for a communal species. I conclude that this species is probably solitary.

Phylogenetic methods are useful not only in determining polarity of evolutionary changes among character states, but also for predicting which species are particularly deserving of study (Packer 1997). Based upon phylogenetic data, the monotypic genus *Thrincohalictus* is thought to be particularly worthy of study because it appears to be the sister taxon to the well studied and behaviourally diverse genus *Halictus* (Eickwort et al. 1996; Packer 1997; Danforth et al. 1999). Thus, this species is particularly important for assessing the pattern of evolution of social behaviour in the bee tribe Halictini.

Thrincohalictus prognathus (Perez) is a relatively large, non-metallic halictine with apical bands of tomentum on the abdominal terga and, as the specific epithet suggests, a long face. It is known, from comparatively few specimens, to occur in Turkey and northern Israel (Bluethgen 1955; Ebmer personal communication) at least as far south as Jerusalem where one male specimen is known from Mt. Scopus.

In May and June 1998 I studied this species in Israel. Although detailed sociobiological analysis requires observation over several months (if not years, Yanega 1988; Sakagami and Packer 1994), some suggestive information can be obtained from samples of dissected bees (Dunn et al. 1999). Additionally, behaviours of bees caught from flowers but forced to interact in artificial arenas (circle tubes) may also be suggestive of social or solitary behavioural ancestry (McConnell-Garner and Kukuk 1997; Wcislo 1997; Paxton et al. 1999; Packer, unpublished observations). In this paper I present data on i) the distribution of *T. prognathus* in Israel, ii) a list of the flowers that it visits, iii) data from dissected and/or measured bees from all available samples and iv) the results of circle tube experiments. The last two sets of data are potentially useful in elucidating the type of social organisation *T. prognathus* might possess.

METHODS

Sampling and phenological assessment.—Most females of *T. prognathus* were collected with a hand net from flowers although some of the pinned specimens included in some analyses were swept from vegetation. Most males were collected while they flew rapidly over bushes or around small trees, presumably in search of females. Some females were pinned but most were preserved in buffered formalin (Pabalan 1998) for subsequent dissection, one was preserved in ethanol for DNA sequencing (Danforth et al. 1999). At two localities, a parking lot and adjacent roadside near a garbage dump near Hazor, and at the peak of Mount Meiron, both in the Upper Galilee, large numbers of females were observed, not all of them were collected. All males were pinned. Flower visitation data were obtained from field samples and, when given, also from pinned specimens.

Bees preserved in formalin were dissected to establish their degree of ovarian development and whether or not they had mated. The fraction of a fully developed oocyte found upon microscopic examination of each of the six ovarioles was estimated by eye. Whether the terminal oocyte was developing or being resorbed was noted. Resorbing oocytes have a fuzzy outline and are often misshapen (Goukon et al. 1988; Pabalan 1998). The spermathecae of inseminated females are opaque whereas those of unmated females are clear and appear like glass bowls.

Head widths of all females (museum specimens and those collected by the author) were measured to ascertain whether there was any seasonal size variation similar to that found in eusocial species in which summer workers are generally smaller than spring gynes (Breed 1975; Packer and Knerer 1985). The number of nicks in one forewing margin was counted to estimate the relative age of specimens. The largest number of nicks counted was 24, consequently, bees with the entire margin slightly eroded were coded as 25 and those with more extensive abrasion coded as 30. Although in reality wing wear measures comparative levels of activity which will not always be directly related to age, it is of some utility. For example, completely unworn individuals will either have recently eclosed or be overwintered females at the early stages of nest initiation and heavily worn individuals will have been active foragers probably for several weeks or more.

Behavioural data.—Despite several days searching in one locality where the species was particularly common (in the vicinity of Hazor in the Upper Galilee), no nest sites were discovered. Behavioural observations were made upon pairs of bees interacting in a "circle tube"—a 20cm long piece of clear plastic with the ends joined together such that moving bees are forced to repeatedly interact with one another (Breed et al. 1978).

Methods generally followed those of earlier authors (Breed et al. 1978; McConnell-Garner and Kukuk 1997; Wcislo 1997b; Paxton et al. 1999; Pabalan et al. submitted) with the exception that bees were placed into circle tubes within ten minutes of capture. This was because it has been discovered that, for some halictines at least, ovarian resorption begins within 30 minutes of captivity (Pabalan 1998 and unpublished observations on *Lasioglossum zephyrum*), suggesting physiological changes are occurring which may be mirrored by altered behavioural interactions among females.

The range of behaviours noted within circle tubes were similar to those often found in other studies (see references above). Bees would sometimes nudge or

Table 1. List of flower records for *Thrincohalictus prognathus.*

Locality	# bees	Flowers
Females		
Mt. Hermon	8	*Nepeta cilicica* Labiatae
Neve Ativ	2	*Lonicera sp.* Caprifoliaceae
	3	*Phlomis chrisophyla* Labiatae
	1	*Cerasus prostrata* Rosaceae
Qiryat Shemona	1	*Papaver* Papaveraceae
Ein Fit	1	*Papaver* Papaveraceae
	1	*Onopordum blanche*
Hazor	dozens	*Centaurea iberica* Asteraceae
	dozens	*Phlomis viscosa* Labiatae
El Rom	3	*Papaver* Papaveraceae
Mt. Meiron	dozens	*Silybum marianum* Asteraceae
Males		
Katzrin	1	*Echinops* Asteraceae
Snir	1	*Vitex anguscastus* Verbenaceae
Ramot Naftali	1	*Ballota saxatilis* Labiatae

lunge at one another, back away from one another either with or without reversing or pass one another, venter to venter, a manoeuvre requiring coordination between individuals. A more aggressive behaviour, the C-posture was also observed. In this stance an individual bends its abdomen forward, beneath the thorax in an apparent attempt at stinging the individual in front of it. It has also been suggested that secretions from the Dufours gland may be released during this posture (Smith and Weller 1989). The occurrence of these behaviours was recorded continuously for 20 (one pair) or 30 (the remaining four pairs) minutes.

RESULTS

Flower records.—Table 1 shows the flower record data for those specimens for which this information was recorded. As can be seen, most of the flowers do not need a long tongue or face for their nectar to be accessible to the bees. However, a few individuals have been collected from long corolla flowers such as the labiate *Nepeta cilicica* and for none of the observations was it definitively recorded whether the bees were collecting pollen or nectar.

Distribution.—Localities where *T. prognathus* was found and also those for which museum records are available are shown in Figure 1. The species appears to be common in northern Israel, particularly in the Upper Galilee and Golan Heights where it occurs at a wide variety of altitudes, from just a few hundred metres above sea level as at Katzrin to over 1,000m at the summit of Mt. Meiron. It has also been collected at 1650m on Mt. Hermon. There is a single male from Jerusalem, collected in the 1940's.

Phenology and dissection data.—Figures 2 and 3 plot head width and wing wear against date of capture for all females available for study. The data are consistent with overwintered females becoming active in March, becoming increasingly worn as they forage through to mid May and with the first individuals of the next generation flying from mid May until June for mating and pre-diapause feeding. Midseason females (worn individuals collected in May) are not smaller than those found earlier in the year (mean head width early bees = 2.31mm, SD = 0.05, $n = 18$; midseason bees = 2.33mm, SD = 0.06, $n = 37$; $t = 1.80$, $p > 0.05$). In fact, in this instance the direction of the size difference is in the opposite direction to that

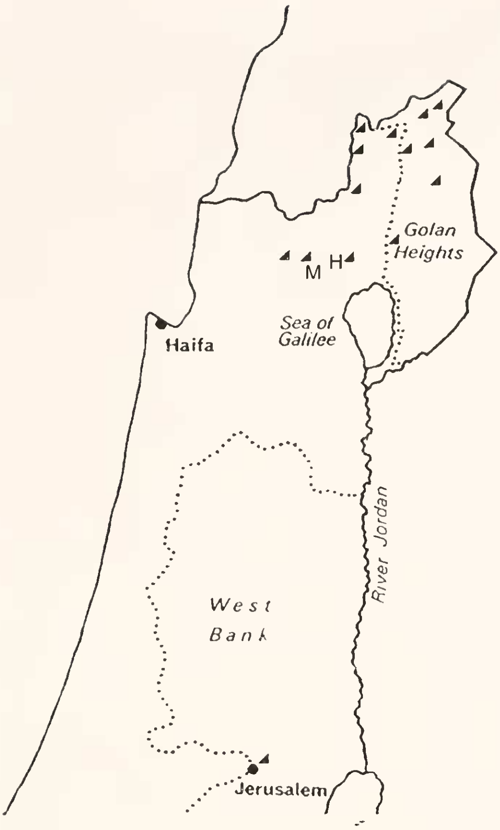

Fig. 1. Map of Israel showing location of sites where *T. prognathus* has been collected. H refers to Hazor and M to Mount Meiron, the two localities where most of the data dealt with in the text were obtained.

expected if midseason bees were workers and early season ones gynes. Similarly, worn late females are no smaller than the unworn pre-overwintering females (Mann-Whitney U test, U = 87, t = 0.39, $p > 0.5$); a size difference would be expected if the worn bees were workers and the unworn ones overwintering future foundresses. Thus, there is no size variation suggestive of the caste differences found in annual eusocial species.

A total of 20 bees from Hazor collected between May 7th and 10th (an additional 10 were pinned) and 17 from Mt. Meiron collected on June 2nd (an additional 8 were pinned) were dissected. All Hazor bees were well worn with an average wing wear of 10.2 (SD = 4.5, n = 30). All formaldehyde preserved bees were mated and had well developed ovaries and 15 of them (75%) had a chorionated oocyte and at least one more ovariole with either a healthy oocyte developing or a sizeable resorbing oocyte. The remaining five bees each contained at least one oocyte three quarters the size of a fully developed one. The average size of the 20 dissected bees was 2.33mm (SD = 0.07) these results change almost imperceptibly when pinned specimens are added to the sample, mean size = 2.32 mm (SD = 0.06, n = 30). No *T. prognathus* were found at Hazor between May 28th and 30th, almost no flowers remained in bloom at this time. These data are consistent with the May Hazor samples being composed of foraging bees which had been active for at least several weeks and which were reproductive individuals. That no males were found suggests that the sample dates preceded the emergence of the next generation.

In contrast, the sample from Mt. Meiron at the beginning of June contained mostly unworn bees (22/25 or 88%) or bees with a total index of wear of one (2/25). Only one bee was well worn and it had 24 nicks in the wing margin. All bees in this sample were mated and all but the heavily worn individual had no ovarian development, large amounts of fat in their abdomens and a crop full of nectar. The exception had two ¾ developed oocytes that were resorbing, its abdomen contained no obvious large fat deposits and its crop was empty. The average size of the Mt. Meiron sample is identical to that of the one from Hazor (mean size = 2.33mm, SD = 0.06, n = 25). These data are consistent with the sampling period having occurred during the emergence phase of the offspring generation with only one individual of the parental generation captured.

None of the bees dissected showed any evidence of oophagy; they did not contain pasty-white material in their guts.

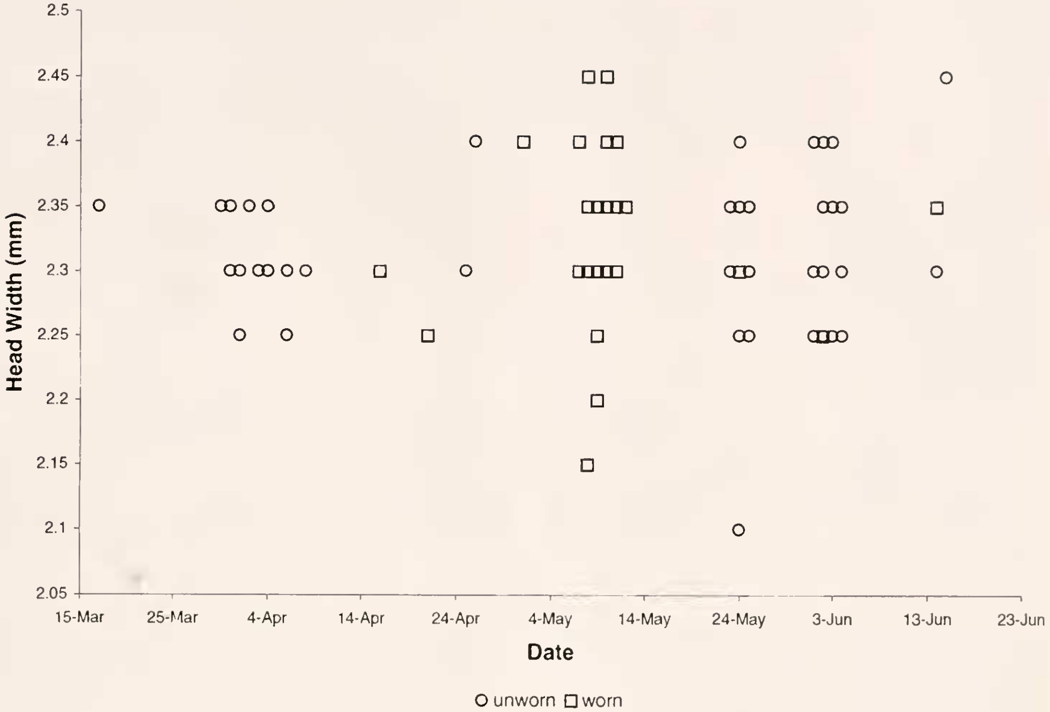

Fig. 2. Head width against collection date for all females, circles represent unworn bees, squares worn ones.

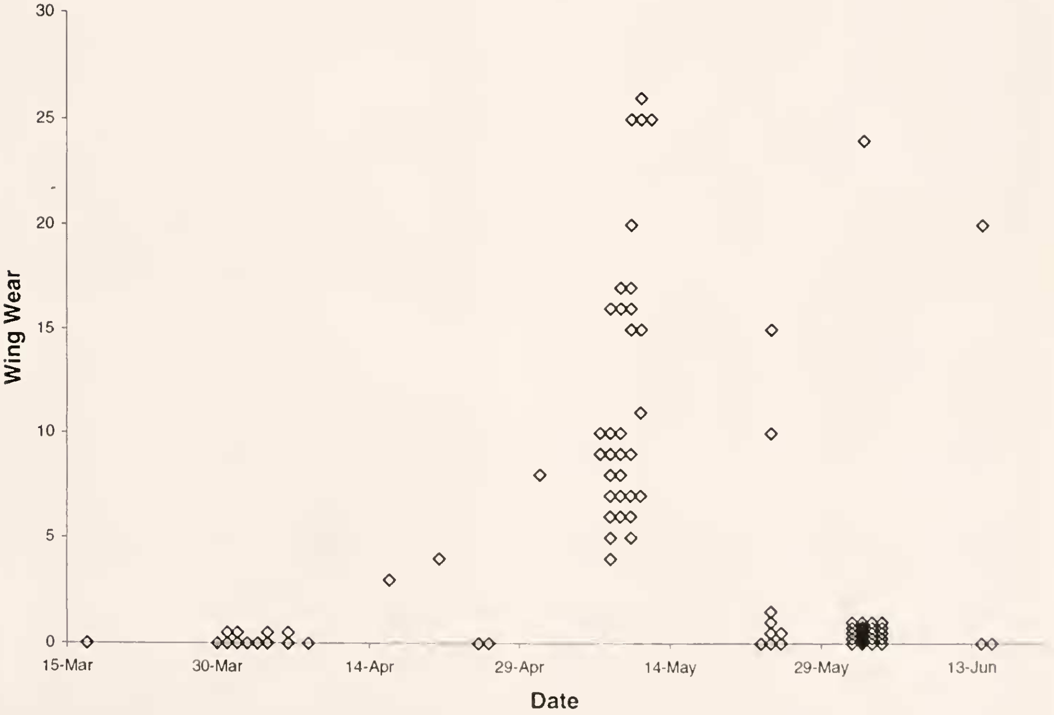

Fig. 3. Wing wear against collection date for all females.

Table 2. Comparison of the frequencies of passing and agonistic interactions among paired individuals of various halictine species. Pass/FE is the frequency of successful passes per frontal encounter, A/FE is the frequency of aggressive interaction per frontal encounter.

Taxon	pss/FE	A/FE	Reference
Eusocial Species			
L. zephyrum queens	0.57	1.28	Breed et al. 1978
L. zephyrum foragers	0.21	0.56	Breed et al. 1978
L. zephyrum guards	0.00	0.61	Breed et al. 1978
Communal Species			
L. hemichalceum	0.81	0.02	Kukuk 1992
Solitary Species			
L. figueresi	0.14	0.41	Wcislo 1997b
L. platycephalum	0.30	0.11	McConnell-Garner and Kukuk 1997
L. (Ctenonomia) sp.	0.33	0.22	
Species With Unknown Behaviour			
T. prognathus	0.03	0.29	this paper

Bees collected and pinned from other samples also have the same size profile as those from samples discussed above, 34 bees from a variety of localities had an average head width of 2.32mm (SD = 0.06).

The first male was found at Ramot Naftali on May 12th, 7 more were found there on June 1st and one was collected at Mt. Meiron on June 2nd. All of these males were comparatively unworn. Few other records are available, but it seems that the first Ramot Naftali specimen is the earliest record and that males may be found until early July (Bluethgen 1955).

Behavioural observations.—A total of 218 encounters between paired bees in five circle tube experiments were observed. Thirty-four of these were C postures, 28 were nudges or lunges and 2 were pushes. Fewer cooperative behaviours were observed: 7 examples of back and follow and 6 successful passes, most of which were preceded by pass attempts; a total of 7 encounters resulted in pass attempts which failed and led to one or both of the bees backing off. Thus, 29.4% of all interactions were classified as antagonistic (varying between 10 and 35% among the pairs) and only 3% were passes (varying between 0 and 7%). The remainder involved one or both bees turning away and may thus be considered as avoidance behaviours. The relative frequency of agonistic and cooperative behaviours did not vary much among the pairs, with the former always exceeding the latter.

Comparisons of successful passes and aggressive acts per encounter are shown in table 2 for those halictines for which such data are available. The behaviour of *T. prognathus* shows the lowest rate of passing (except for guard:guard pairs in *L. zephyrum*) and a level of aggressive interaction that falls within the range for solitary species and outside that for either communal or eusocial taxa.

DISCUSSION

Thrincohalictus prognathus has been considered to be a rare species likely to have a preference for flowers with a long corolla. However, observations in northern Israel confirm that it is widespread (Figure 1) and often common and that it does not have a preference for long tubular flowers (Table 1).

In solitary and communal halictine bees, all individuals in a sample collected from flowers may be expected to be of similar age (except during a period of overlap of generations) and show similar evidence of reproductive activity. Early season samples should be of mostly unworn bees with average wear increasing monotonically until late in the season when the young offspring generation individuals fly to mate and to forage to fill their crops with nectar. At this time, bimodality in wear may be expected if some of the parental generation individuals have survived and are active. In samples of a eusocial species, early samples may be expected to show evidence of reproduction and comparatively little heavy wear, mid-season samples should show varying proportions of reproductively inactive individuals and a wide range of indices of wear and the latest samples should comprise mostly unworn pre-diapause females and some heavily worn ageing workers. Additionally, bees in samples of eusocial species taken in mid season should average smaller than those collected in spring as workers are usually smaller than nest foundresses (Breed 1975) (although the size difference varies from requiring large sample sizes to achieve statistical significance (Eickwort 1985) to being non-overlapping such that individuals can be classified as queens or workers on size alone (Knerer 1992)).

The samples of *T. prognathus* show no evidence of eusociality. The earliest specimen found was collected in mid March. Most samples are from early May and bees at this time are well worn but show substantial and largely equivalent levels of reproductive development. No unmated or ovarially undeveloped individuals have been detected at this time, which, being just prior to the apparent emergence of the overwintering brood, should have consisted entirely, or almost entirely, of workers if the species were eusocial. Although data on recently emerged brood are mostly from a separate and higher altitude (though nearby) locality, they indicate that foraging by females of this species has ceased by early June and that males are actively searching for overwintering females at this time. In most of the region under discussion here, there are almost no flowers available for bee foraging after early June. Indeed, there was an extremely marked deterioration of forage availability at Hazor between early May and the end of the month such that great bee abundance had changed to an almost complete absence, several hours of searching between May 28th and 30th failed to result in any *T. prognathus* being found whereas earlier in the month several dozens could be observed in an hour.

Thus, based upon phenology, dissection and wear data, I conclude that *T. prognathus* is not an eusocial species in Israel. I now turn to the behavioural interactions among individuals observed in circle tubes.

Behavioural profiles of bees in circle tubes seem to reflect the differences between the conflictive relationships in eusocial and semisocial societies and harmonious interactions in communal ones (Kukuk and Crozier 1990; McConnell-Garner and Kukuk 1997; Paxton et al. 1999). In eusocial societies, where competition among individuals over oviposition or the sex ratio of brood occurs, agonistic acts such as C-postures, lunges and pushing are common (McConnell-Garner and Kukuk 1997; Pabalan et al. submitted). Conversely, communal species are much more tolerant, pass one another readily (Paxton et al. 1999) and unrelated individuals have even been observed performing trophallaxis (Kukuk and Crozier 1990). Solitary species show intermediate levels of both aggressive and cooperative behaviours (Table 2).

As noted above, the phenological and dissection data suggest that *T. prognathus* is not eusocial or semisocial. Similarly, communal behaviour would seem to be unlikely as the pass per encounter rates of bees with this type of colony organisation are consistently high (McConell-Garner and Kukuk 1997; Packer unpublished observations) yet in *T. prognathus* they are the lowest recorded except for pairs of guards which are expected not to pass one another. Thus, I conclude that the data are most consistent with the hypothesis that this species is solitary. Clearly more detailed information is required and knowledge of the nest architecture of *T. prognathus* would also be of interest.

In conclusion, *T. prognathus* would seem to be a locally abundant halictine in northern Israel, it does not seem to specialise on pollen or nectar from long corolla plants and its phenology and behavioural patterns in experimental arenas are consistent with it being a solitary species, although forms of quasisocial behaviour cannot be definitively disproven.

ACKNOWLEDGMENTS

I thank Drs. Amnon Freidberg, Abraham Hefetz and Avi Shmida for facilitating my studies in Israel, and, in particular, Rani Kasher and his family for accommodation during the study reported here and to Rani for access to his collection and for identifying the plants visited by *T. prognathus*. Jessica Janjic helped with the figures and Dr. J. Shore provided phytosystematic information. Financial support came from the Natural Sciences and Engineering Research Council of Canada.

LITERATURE CITED

Bluethgen, P. 1955. The halictinae (Hymen., Apoidea) of Israel I. Genus *Halictus* (Subgenera *Halictus* s.str. and *Thrincohalictus*). *Bulletin of the Research Council of Israel* 5: 5–23.

Breed, M. D. 1975. Sociality and seasonal size variation in halictine bees. *Insectes Sociaux* 22: 375–380.

Breed, M. D., J. M.Silverman and W. J. Bell. 1978. Agonistic behavior, social interactions and behavioral specialization in a primitively eusocial bee. *Insectes Sociaux* 25: 351–364.

Danforth, B. N., H. Sauquet and L. Packer. Phylogeny of the bee genus *Halictus* (Hymenoptera: Halictidae) based on parsimony and likelihood analyses of EF-1alpha sequences. *Molecular Phylogenetics and Evolution* 13: 605–618.

Dunn, M., P. L. Mitchell and L. Packer. 1999. Phenology and social biology of two sibling species of *Halictus* in an area of sympatry. *Canadian Journal of Zoology* 76:

Eickwort, G. C. 1986. First steps into eusociality: the sweat bee *Dialictus lineatulus*. *Florida Entomologist* 69: 742–754.

Eickwort, G. C., K. R. Eickwort, J. M. Eickwort, J. Gordon and A. Eickwort. 1996. Solitary behavior in a high-altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). *Behavioral Ecology and Sociobiology* 38: 227–233.

Goukon, K., Y. Maeta and S. F. Sakagami. 1988. Seasonal changes in ovarian state in a eusocial halictine bee, *Lasioglossum duplex*, based on stages of the oldest oocytes in each ovariole (Hymenoptera: Halictidae). *Research in Population Ecology* 29: 255–269.

Knerer, G. 1992. The biology and social behaviour of *Evylaeus malachurus* (K.) (Hymenoptera; Halictidae) in different climatic regions of Europe. *Zoologische Jahrbucher Abteilung fur Systematik, Oekologie und Geographie der Tiere* 119: 261–290.

Kukuk, P. F. 1992. Social interactions and familiarity in a communal halictine bee *Lasioglossum (Chilalictus) hemichalceum*. *Ethology* 91: 291–300.

Kukuk, P. F. and R. H. Crozier. 1990. Trophallaxis in a communal halictine bee *Lasioglossum (Chilalictus) erythrurum*. *Proceedings of the National Academy of Sciences U.S.A.* 87: 5401–5404.

McConnell-Garner, J. and P. F. Kukuk. 1997. Behavioral interactions of two solitary halictine bees with comparisons among solitary, communal and eusocial species. *Ethology* 103: 19–32.

Pabalan, N. A. 1998. *Aspects of the interaction between reproductive morphology and social behaviour of a primitively eusocial sweat bee,* Halictus ligatus *Say (Hymenoptera; Halictidae).* Unpublished Ph.D. thesis, York University, Toronto. 149pp.

Pabalan, N., K. G. Davey and L. Packer. Escalation of aggressive interactions during staged encounters in *Halictus ligatus* (Hymenoptera: Halictidae). *Journal of Insect Behavior*. Submitted.

Packer, L. 1997. The relevance of phylogenetic systematics to biology: examples from medicine and behavioral ecology. p11–29. In P. Grandcolas (ed). *The Origin of Biodiversity in Insects: Phylogenetic Tests of Evolutionary Scenarios. Mémoires du Muséum National d'Histoire Naturelle vol. 173.* 360pp.

Packer, L. and G. Knerer. 1985. Social evolution and its correlates in bees of the subgenus *Evylaeus* (Hymenoptera: Halictidae). *Behavioral Ecology and Sociobiology* 18: 363–375.

Paxton, R. J., P. F. Kukuk and J. Tengo. 1999. Effects of familiarity and nestmate number on social interactions in two communal bees, *Andrena scotica* and *Panurgus calcaratus* (Hymenoptera, Andrenidae). *Insectes Sociaux* 46: 109–118.

Sakagami, S. F. and L. Packer. 1994. Delayed eusociality in halictine bees. p. 86 In: Lenoir, A., G.

Arnold and M. Lepage (eds). *Les Insectes Sociaux.* Paris, Universite Paris Nord. 583pp.

Smith, B. H. and C. Weller. 1989. Social competition among gynes in halictine bees: the influence of bee size and pheromones on behavior. *Journal of Insect Behavior* 2: 397–411.

Wcislo, W. T. 1997. Elements of dominance behavior and social interactions in a solitary bee *Lasioglossum (Dialictus) figueresi* (Hymenoptera: Halictidae). *Insectes Sociaux* 44: 199–208.

Yanega, D. 1988. Social plasticity and early-diapausing females in a primitively eusocial bee. *Proceedings of the National Academy of Sciences U.S.A.* 85: 4374–4377.